Assessing Avian Predation on Juvenile Salmonids using Passive Integrated Transponder Tag Recoveries and Mark–Recapture Methods

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Abstract

Many populations of coho salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* are listed under the U.S. Endangered Species Act. Until recently, the role of avian predation in limiting recovery of coho salmon and steelhead in central California coastal watersheds has been overlooked. We used recoveries of passive integrated transponder (PIT) tags from Año Nuevo Island (ANI), a breeding site for several species of piscivorous seabirds, to estimate predation rates on juvenile salmonids and identify susceptible life stages and species responsible for predation. A total of 34,485 PIT tags were deployed in coho salmon and steelhead in six watersheds in San Mateo and Santa Cruz counties. Tags were deposited on ANI by predators after ingestion of tagged fish. Because tags were not removed

from the island and were detected on multiple sampling occasions, we were able to use mark–recapture models to generate a corrected minimum predation estimate. We used POPAN, a variation of the Jolly–Seber model, to generate an estimate of gross population abundance, which accounted for tags deposited on the island but not detected during surveys. Detections of 196 tags from surveys conducted between autumn 2006 and spring 2009 were incorporated into the model, producing a gross population estimate of 242 tags (SE = 9.8). Addition of tags detected between autumn 2009 and 2010 to the abundance estimate from POPAN produced a new minimum estimate of 362 tags on ANI. Western gulls *Larus occidentalis* probably were the primary predator depositing tags on ANI. Minimum predation estimates ranged from 0.1% (Soquel Creek) to 4.6% (Waddell Creek) of outmigrating coho salmon and steelhead smolts. Predation was potentially greater given still unquantified deposition of tags off-colony and destruction of tags during digestive processes of predators. Finally, avian predators targeted estuary-reared fish, which contributed disproportionately to adult populations, further impacting imperiled salmon populations.

Pacific salmonids *Oncorhynchus* spp. are commercially valuable but have decreased in number throughout much of their range. Currently many runs in the eastern Pacific Ocean are listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (Gustafson et al. 2007). Decreases often are attributed to the "four-H's": overharvest, obstruction of migratory routes by hydropower facilities, habitat degradation, and hatchery propagation (Collis et al. 2001; Good et al. 2007). There is increasing appreciation, however, that additional factors exacerbate salmon declines (e.g., Ruggerone 1986; Good et al. 2007; Sanderson et al. 2009). For example, salmonids are eaten by piscivorous birds, fish, and mammals and are vulnerable to predation during all life history stages (Collis et al. 2001; Weise and Harvey 2005; Wright et al. 2007).

Predation on juvenile salmonids by seabirds has been well documented in large river systems, for example, in the Columbia and Sacramento rivers, and efforts have been made to quantify the extent of avian predation (Ruggerone 1986; Collis et al. 2001; Roby et al. 2003; Major et al. 2005; Good et al. 2007). For example, ring-billed gulls *Larus delawarensis* and California gulls *L. californianus* consumed approximately 10.3% of all juvenile salmonids passing dams on the Yakima River, a tributary of the Columbia River (Major et al. 2005). Juvenile salmonids comprised approximately 75% of the diet of Caspian terns *Sterna caspia* and 50% of the diet of double-crested cormorants *Phalocrocorax auritas* nesting on an artificial dredge-spoil island in the lower Columbia River (Roby et al. 2003). Avian predators ate as many as 4–12 million of the 60–100 million salmonid smolts out-migrating through the Columbia River estuary annually, leading to management actions designed to lessen the effects of predation (Roby et al. 2003; Good et al. 2007). More recently, coded wire tags were used to estimate Caspian tern predation on salmonids originating in the Sacramento–San Joaquin River system (Evans et al. 2011).

In contrast to the body of literature quantifying predation on salmonids by avian species in large river systems, comparable studies in small coastal watersheds in California are lacking from the published literature. Coastal watersheds south of San Francisco Bay, California, provide spawning and rearing habitat for endangered coho salmon *O. kisutch* and steelhead *O. mykiss*. Although diversion of water for human use, degradation of local habitat, and changes in ocean productivity are the major reasons for the continued decrease of Central Coast coho salmon and steelhead (Good et al. 2005), it remains unknown whether predation may be affecting the status of these populations and hindering future recovery. Given the extent of avian predation on salmonids in the Columbia River basin, and associated implications for recovery of federally listed runs, quantifying the magnitude of predation and identifying susceptible life stages was considered a necessary step in understanding factors limiting the recovery of salmonids in California.

Recovery of salmon tags on roosting and breeding sites used by piscivorous birds has increasingly been used to document predation. For example, detection of passive integrated transponders (PIT tags) on seabird colonies was used to document and quantify predation on salmonids by piscivorous birds in the Columbia River basin (Collis et al. 2001; Ryan et al. 2001; Roby et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Although an unknown proportion of tags may be damaged during the digestive process, PIT tags are capable of remaining functional through ingestion of a tagged fish by piscivorous birds and mammals and subsequent defecation or regurgitation at breeding or roosting sites. Since 2002, PIT tags were used to enhance the understanding of population biology and marine survival of coho salmon and steelhead in six watersheds within Santa Cruz and San Mateo counties (e.g., Hayes et al. 2004, 2008, 2011; Bond et al. 2008). In 2006, one of these PIT tags was recovered on Año Nuevo Island (ANI), a seabird and marine mammal breeding colony located in San Mateo County, California (37°6′N, 122°20′W), which prompted the initiation of annual scans for PIT tags on ANI with the objectives of (1) quantifying predation on salmonids by piscivorous birds and marine mammals, (2) identifying life stages most susceptible to predation, and (3) identifying predators responsible for depositing tags on ANI.

Recovery of PIT tags only allows for minimum estimates of predation because (1) an unknown number of tags are deposited away from breeding and roosting areas, (2) some tags may lose function during the process of ingestion and excretion, (3) some tags may lose function after deposition on the island, and (4) not all tags on a colony are detected (Collis et al. 2001; Ryan et al. 2001). We addressed uncertainties from

(3) and (4) by the novel application of mark–recapture statistics to improve our minimum estimate of predation on juvenile salmonids. Mark–recapture approaches generally are applied to generate estimates of population parameters including survival (Lebreton et al. 1992), abundance (Jolly 1965; Seber 1965), and rate of population change (Pradel 1996). Because PIT tags were uniquely numbered, not removed from ANI after detection, and often detected during subsequent trips to the island, it was possible to use mark–recapture statistics to estimate population parameters associated with the population of tags (representing the number of salmonids eaten and deposited by predators) on ANI. We used mark–recapture statistics to create a correction factor to apply to PIT tags detected on ANI between 2006 and 2009 to improve minimum estimates of the number of salmonids eaten by predators using ANI as breeding and resting habitat. Our approach will provide the first steps in understanding the effects of avian predation on ESA-listed coho salmon and steelhead in coastal watersheds near their contemporary southern range extent and may help inform recovery plans for these imperiled populations.

METHODS

Study site.—This study took place in central California and focused on Año Nuevo Island, which provides breeding habitat for several species of piscivorous seabirds and marine mammals. The island is located in close proximity to several watersheds that support coho salmon and steelhead. Año Nuevo Island is 10 ha in size and located 1.6 km off Point Año Nuevo, San Mateo County, California (Figure 1). Piscivorous species that used elevated portions of the island that could be scanned for PIT tags included western gulls *L. occidentalis*, Brandt's
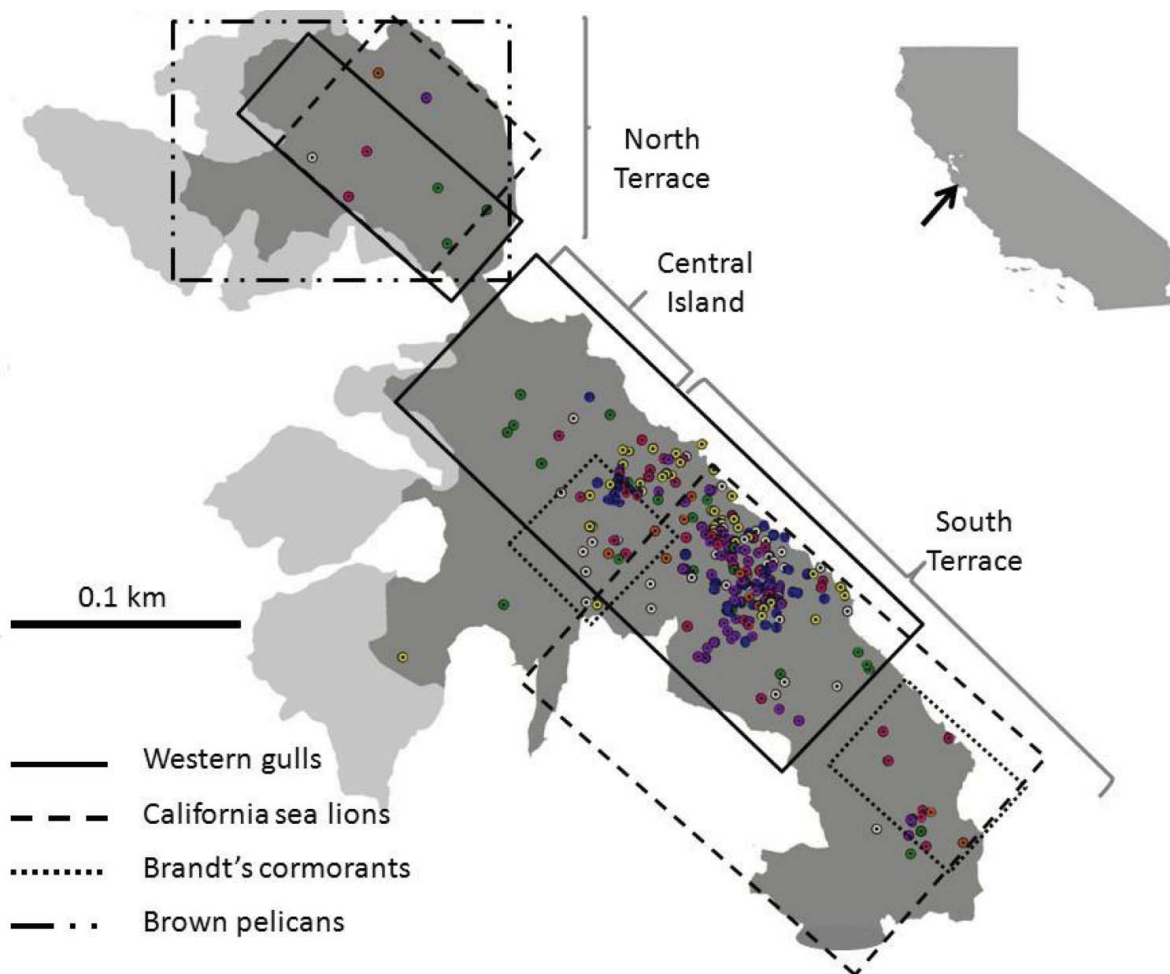
FIGURE 1.   Location of coho salmon and steelhead PIT tags on Año Nuevo Island, by year of detection, 2006–2010. Elevated portions of the island scanned for PIT tags are dark gray, intertidal areas not scanned are light gray, surrounding water is white, and circles represent tag locations. Colors correspond to the year a tag was first detected (white = 2006, yellow = 2007, green = 2008, pink = spring 2009, orange = autumn 2009, blue = spring 2010, purple = autumn 2010). Western gulls (solid lines), and sea lions (heavy dashes) are ubiquitous over areas of the island scanned for PIT tags; approximate areas of greatest density are shown. Approximate areas used by Brandt's cormorants (light dashes), and brown pelicans (short and long dash combination) also are shown. [Figure available in color online.]

cormorants *P. penicillatus*, pelagic cormorants *P. pelagicus*, brown pelicans *Pelicanus occidentalis*, California sea lions *Zalophus californianus*, and Steller sea lions *Eumetopias jubatus*. Populations of western gulls and Brandt's cormorants that breed on ANI have increased in recent decades. During 1998, an estimated 1,274 western gulls and 664 Brandt's cormorants bred on ANI; by 2007, the estimated number of birds breeding on ANI had reached 2,196 western gulls and 3,660 Brandt's cormorants (Point Reyes Bird Observatory [PRBO], unpublished data). Although gulls and cormorants are present year-round, numbers are greatest during breeding (spring and early summer), after which adults disperse. Gulls generally disperse in September and cormorants in July–August (Pierotti and Annett 1995; Wallace and Wallace 1998). Brown pelicans breed in southern California and Baja California and are present in central California during the nonbreeding period between June–July and December (Shields 2002). During the nonbreeding period, brown pelicans roost on ANI with greatest numbers counted during July and August except in years when breeding attempts were unsuccessful, and pelicans arrived on ANI in April or May (Shields 2002; Thayer and Sydeman 2004; PRBO, unpublished data). The number of pelicans using ANI varies considerably among years (PRBO, unpublished data). Steller's sea lions breed on ANI and occur in fewer numbers compared with California sea lions that use ANI for resting habitat during the nonbreeding season. Although California sea lions are present on ANI year-round, numbers vary considerably within and among years (P. Morris, University of California Santa Cruz, personal communication). For example, the mean number of California sea lions on ANI during near-monthly aerial surveys (between May 1997 and September 1998) was 3,145 animals and ranged from 510 in June 1997 to 5,963 in June 1998 (Weise 2000).

PIT tag detections.—Beginning in 2006, we scanned ANI for PIT tags annually using a portable PIT tag antenna system modified from the instream PIT tag antenna described by Bond et al. (2007). The system was capable of detecting 134.2-kHz full duplex PIT tags (Bond et al. 2007). The portable, pole-mounted, circular antenna was powered by a 6-V battery and carried in a backpack along with a data logger. Tag identity and time detected were logged for each tag. A portable GPS unit was carried during each scan of the island beginning in 2007, allowing GPS coordinates to be assigned to each tag detected. The GPS positions were logged at 2-s intervals to evaluate the land area covered and to ensure that coverage of the island was adequate and consistent among surveys. Deployment histories of most PIT tags detected on ANI were known, so it was possible to determine the species, date, and location of initial tagging, subsequent dates fish were captured (for all watersheds), life stage at tagging (juvenile or adult), and any detections of fish by instream PIT tag antennas (Scott Creek only). Surveys for tags were conducted in late autumn–early winter during 2006, 2007, and 2008 and in spring and late autumn–early winter of 2009 and 2010 (see Table A.1.2 for survey dates).

Correction factor analysis.—We applied a modeling framework to improve estimates of predation on juvenile salmonids obtained from deposition of PIT tags on ANI. We used the model to generate a correction factor to account for loss of PIT tags from ANI between sampling events. Tag loss could occur through erosional processes, tag breakage and loss of tag function, tag interference, and burial out of range of scanning antennas (Collis et al. 2001; Ryan et al. 2001). We used the POPAN (Schwarz and Arnason 1996) formulation of the Jolly–Seber mark–recapture model for open populations to estimate the gross population size of tags on ANI, which served as a corrected estimate of minimum tag deposition on the island. We selected the POPAN model because PIT tags on ANI represent a distinct, open population of individual fish with PIT tags that were eaten by predators and deposited on the island through regurgitation or defecation. Additionally, the estimates of gross recruitment produced by POPAN allowed us to account for tags deposited on the island that were subsequently lost through physical tag loss or tag breakage before the next sampling interval (Arnason and Schwarz 2002). Modeling was conducted within the framework of Program MARK version 5.1 (White and Burnham 1999), and model notation followed Arnason and Schwarz (2002).

Key assumptions of the POPAN model are: (1) tags are retained throughout the experiment and are read properly; (2) sampling is instantaneous relative to the study period; (3) catchability and survival of marked and unmarked individuals are homogeneous; and (4) the study area did not change in size during the course of the study (Lebreton et al. 1992; Arnason and Schwarz 2002). Locations of tags were mapped after each survey of the island, so areas of the island with high tag deposition were known. All areas of the island were allocated equal effort during surveys regardless of tag densities to avoid biases associated with heterogeneous catchability (Lebreton et al. 1992).

Four fundamental parameters were generated using POPAN: (1) survival (Φ_i), interpreted as the probability that a tag initially deposited at ANI was not lost from the island or destroyed between sampling at time i and time $i + 1$ (given that the tag was in the population and available to be detected); (2) probability of capture (p_i), interpreted as the probability of detecting a given tag during a complete scan of the island at time i; (3) superpopulation size (N), which was the pool of all tags deposited on ANI (total net recruitment, Arnason and Schwarz 2002); and (4) proportion of tags from the superpopulation that entered the island population (b_i) after time i that survived to time $i + 1$ (Arnason and Schwarz 2002). In addition, four other parameters of interest were derived from the fundamental parameters: (1) gross recruitment (B_i^*), which accounts for tags that entered the population after time i but were lost from the population before the next sampling interval at time $i + 1$; (2) net births (B_i), defined as the number of tags that entered the population after time i and survived to time $i + 1$; (3) abundance at time i (N_i); and (4) total gross population size (N^*), which includes
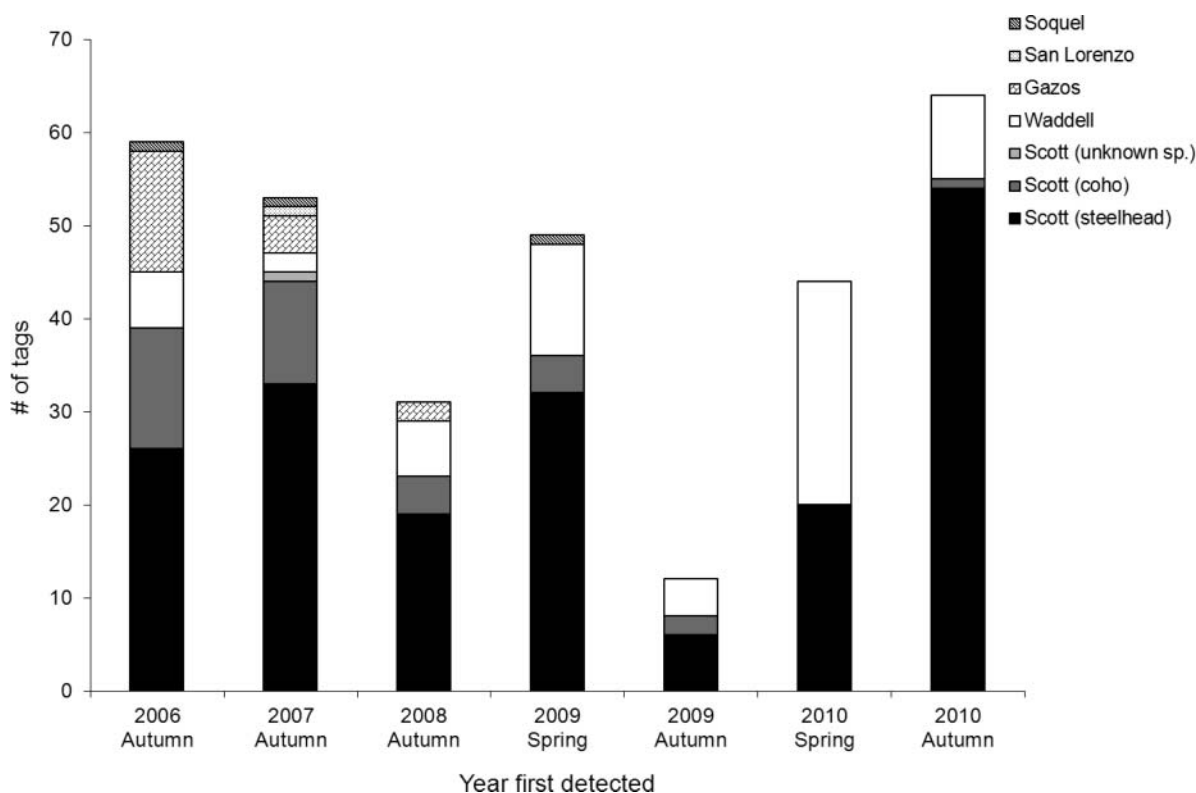
FIGURE 2. PIT tags detected on Año Nuevo Island by watershed of origin, salmonid species, and year first detected between 2006 and 2010. Tags from Soquel, San Lorenzo, Gazos, and Waddell watersheds were from steelhead only.

tags deposited on ANI that were lost from the population before sampling (Schwarz et al. 1993; Arnason and Schwarz 2002). This measure of gross population size served as our corrected minimum estimate of tag deposition onto ANI during the study period.

A candidate set of eight models was created in which survival (Φ_i), probability of capture (p_i), and probability of entry (b_i) parameters were either held constant ($\cdot$) or allowed to vary with time (t). When fitting the candidate models, the logit link function was used for the parameters Φ_i and p_i and the log link function was used for the parameter N. The set of b_i parameters must sum to ≤ 1, so the multinomial logit link function was used to constrain the b_i parameters to facilitate convergence (Schwarz and Arnason 1996; White and Burnham 1999). Models were compared using Akaike's information criterion, adjusted for small sample sizes (AIC_c). The most parsimonious model received the lowest AIC_c value. The relative fit of models in the candidate model set was assessed by comparing AIC_c weights (Burnham and Anderson 2002). We applied a χ^2 goodness-of-fit test to the fully time-dependent model to assess model fit. Goodness-of-fit testing was accomplished using Program RELEASE (Burnham et al. 1987), run within Program MARK version 5.1 (White and Burnham 1999). If lack of fit was detected a variance inflation factor ($\hat{c} = \chi^2/\mathrm{df}$) was applied to the model set and quasi-Akaike's information criterion (QAIC) was used for model comparison (Lebreton et al. 1992).

RESULTS

Between autumn 2006 and autumn 2010, we detected 316 unique PIT tags on ANI (Figure 1) out of 34,485 wild and hatchery coho salmon and steelhead tagged in five watersheds in Santa Cruz County (Waddell, Scott, San Lorenzo, Soquel, and Aptos) and one watershed in San Mateo County (Gazos) (Table A.1.1). It was possible to determine the identity of 312 of the PIT tags detected on ANI using known deployment history data (Figure 2). Four tags were from salmonids (all steelhead from Scott Creek) that were last handled as adults (mean fork length [FL], 40.3 cm; SD = 2.4); however, the majority of tags detected were from juvenile steelhead (88%; 273 out of 312). Only 11% of the tags detected on ANI were from juvenile coho salmon. Tagging effort for juvenile coho salmon was extremely variable during the years encompassed by this study, whereas tagging effort was more consistent for steelhead. Because of the variation in tagging effort and the low recovery rate of PIT tags from coho salmon on ANI (35 tags), detections of tags from coho salmon and steelhead were combined and analyzed together for generating the correction factor.

Tags detected were from salmonids originating in five of the six watersheds where PIT tags were deployed (Figure 2). Although PIT tags were deployed in Aptos Creek, no tags from this watershed were detected on the island. The greatest number of PIT tags on ANI ($n = 226$) were from fish that originated in Scott Creek (Figure 2). For this watershed, we identified the species,
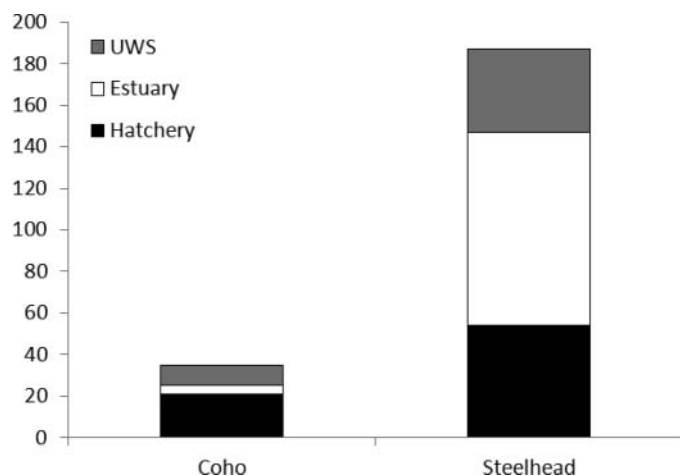
FIGURE 3. Number of PIT tags from juvenile coho salmon and steelhead on Año Nuevo Island that originated in Scott Creek, by origin. Hatchery fish were tagged and released from a hatchery located in Scott Creek. Coho salmon and steelhead of wild origin were tagged in the upper watershed (UWS) upstream from the estuary influence, or in estuary habitat.

origin (hatchery or natural), and location in the watershed where fish were tagged (Figure 3). Four fish, all steelhead, were known to be adults prior to tag detection on ANI; the remaining 222 fish were juvenile coho salmon or steelhead. Twenty-eight percent of PIT tags from juvenile steelhead (54 of 187) and 60% of juvenile coho salmon were of hatchery origin (21 of 35). Seventy percent of wild steelhead (93 of 133) and 28% of wild coho (4 of 14) were tagged in the Scott Creek estuary, whereas 30% of wild steelhead (40 of 133) and 72% percent of wild coho salmon (10 of 14) were tagged in the upper watershed above the influence of the estuary.

The majority of tags detected during all years (approximately 90%) on ANI were located in an area of the south terrace used by western gulls for breeding (Figure 1). Approximately 7% of tags were located in areas used by Brandt's cormorants for breeding, but these areas also were used by western gulls and sea lions (P. Morris, University of California at Santa Cruz, personal communication). The remaining 3% of tags were detected in an area used by western gulls and brown pelicans. California sea lions are ubiquitous over areas of the island scanned for PIT tags; thus, they also use the north and south terraces of ANI where tags were found (P. Morris, personal communication).

Correction Factor Analysis

Complete scans of ANI were conducted during autumn 2006, 2007, and 2008 and spring 2009. The areas surveyed during autumn 2009 and spring and autumn 2010 were not comparable with previous scans of the island. In autumn 2009 we experienced an equipment failure that resulted in a nonquantifiable loss of sensitivity. During spring 2010 the area surveyed was reduced physically to prevent disturbance of cormorants and sea lions, whereas effort was increased during autumn 2010 as part of an associated study. Consequently, data collected in autumn

2009, spring 2010, and autumn 2010 were not included in the estimation of tag abundance using POPAN (as this would under- or overestimate abundance and associated parameters, Arnason and Schwarz 2002). We ran the model with tags detected in the reduced area of the island scanned during spring 2010 (using detections from 2006 to spring 2009, and spring and autumn 2010). However, data were too sparse to test model goodness of fit, and the estimated tag abundance differed from the original model (2006 to spring 2009 for the entire island) by less than 1%. We therefore chose to use the original model (2006 to spring 2009 for the entire island) to generate our corrected minimum estimate of predation.

Tag detections from complete surveys (autumn 2006, 2007, and 2008 and spring 2009; all detections: $n = 358$, unique tags: $n = 196$) were incorporated into the POPAN model (Schwarz and Arnason 1996). The unequal sampling intervals created by sampling in autumn (2006, 2007, and 2008) and spring (2009) were accounted for within the Program MARK framework, so estimates of survival rates are presented on a per-time basis. The goodness-of-fit test indicated lack of overall model fit ($\chi^2 = 14.5$, $P = 0.006$). The assumption of homogeneous capture probability was met (Test 2C.2, Table A.2.1); therefore, the lack of model fit stemmed from overdispersion or failure to meet the assumption of homogeneous survival. The assumption of homogeneous survival had two components: (1) the probability that an individual alive at occasion i was seen again was independent of whether it was marked on or before occasion i, and (2) timing of subsequent detections of individuals was independent of whether they were marked on or before occasion i. Component (1) of the assumption of homogeneous survival was met (Test 3.SR2 and 3, Table A.2.1); however, component (2) was not met (Test 3.Sm2, Table A.2.1) because a great number of individuals (18) were detected during all four surveys of ANI (see Appendix 2 for a discussion of how this was determined). Although it was not possible to determine whether lack of fit stemmed from heterogeneity of survival or overdispersion, the variance inflation factor ($\hat{c}$) for our model was 3.6, indicating that model structure was reasonably adequate (Lebreton et al. 1992). To account for overdispersion, therefore, we applied the variance inflation factor of 3.6 to the resulting model set (Lebreton et al. 1992).

The model that best fit the data (i.e., received the lowest $QAIC_c$ score) had constant probability of survival and probability of capture and time-variant probability of entry (Table 1, Model A). Based on comparison of the $QAIC_c$ weights, support for this model was 6.2 times greater than the next best model (Table 1, Model B). Probability of survival (Φ) was 0.8578 (95% confidence interval [CI], 0.6504–0.9513), probability of capture (p) was 0.6436 (95% CI, 0.4715–0.7853), and the superpopulation size (N) was 233.29 (Table 2). Because the best-fit model predicted constant capture (p) and survival (Φ), all fundamental and derived parameters were estimable (Schwarz and Arnason 1996). Although it was not possible to directly measure efficiency of PIT tag scanning equipment, the constant probability of capture indicated that scanning effort and PIT tag antenna

TABLE 1. Comparison of candidate POPAN models used to estimate abundance, survival, recapture, and entry parameters for salmonid PIT tags on Año Nuevo Island (2006–Spring 2009). AIC_c = Akaike's information criterion adjusted for small sample sizes, ΔAIC_c = difference in AIC_c between the AIC_c for a given model and the AIC_c for the best-fit model, AIC_c weight = Akaike weight indicating the relative support for a model based on AIC_c, Φ_i = probability of survival, p_i = probability of capture, b_i = probability of entry, t = time, NA = not applicable. Numerical convergence was not reached for models G and H.

Model identification	Model	AIC_c	ΔAIC_c	AIC_c weight	Number of parameters
A	$\Phi(.)p(.)b(t)$	136.27	0	0.81	6
B	$\Phi(t)p(.)b(t)$	139.90	3.64	0.13	8
C	$\Phi(.)p(t)b(t)$	141.93	5.66	0.05	9
D	$\Phi(t)p(t)b(t)$	145.85	9.58	0.01	11
E	$\Phi(t)p(.)b(.)$	22,629.92	22,493.65	0	6
F	$\Phi(.)p(.)b(.)$	22,631.51	22,495.24	0	4
G	$\Phi(.)p(t)b(.)$	NA			
H	$\Phi(t)p(t)b(.)$	NA			

efficiency were relatively consistent among surveys. The difference between gross recruitment (B_i^*) and net recruitment (B_i) provides an estimate of tags that were deposited on ANI between sampling events but were lost from the tag population before they could be detected, and ranged from two to four tags (Table 3). Gross population size (N^*) was 242 PIT tags (SE = 9.8; Table 3). This means that although only 196 tags were detected on the island between 2006 and spring 2009, 242 tags were probably deposited on the island through spring 2009. When added to the raw number of tags detected between autumn 2009 and autumn 2010 (120 tags), our corrected, minimum estimate of deposition on ANI was 362 tagged fish.

To apply our correction factor to individual watersheds, we multiplied the new corrected estimate of tag deposition (362 tags) by the percentage of tags detected on the island for each watershed (Table 4). This approach was taken because the number of tags detected on ANI from fish tagged in Scott Creek ($n = 226$) was 2.5 times greater than the number of tags recovered from all other watersheds combined ($n = 89$); therefore, data were too sparse to run the POPAN model with data grouped by watershed. By applying this correction factor, there was no increase in the number of fish originating from the San Lorenzo watershed and Soquel Creek in the ANI tag population

(Figure 3). New estimates of total tags originating from Scott Creek (260), Gazos Creek (22), and Waddell Creek (72) were obtained when the correction factor was applied, increasing the minimum predation rates for these watersheds to 0.94% for Scott Creek, 2.9% for Gazos Creek, and 4.6% for Waddell Creek (Figure 4).

TABLE 3. Estimates of derived parameters from the best fit model [$\Phi(t)p(.)b(t)$]. Gross births (B_i^*) = number of tags arriving on the island between each pair of years; Net births (B_i) = number of tags arriving on the island between each pair of years that survive to time $i + 1$, $B_i^* - B_i$ = difference between gross and net births, Abundance (N_i) = abundance of tags in the island population during each survey, Gross population size (N^*) = all tags deposited on the island including tags deposited but lost from the island before sampling. Estimates for each parameter are presented with associated standard error (SE) and upper and lower 95% confidence limits (CL).

Parameter	Parameter estimate	SE	Lower 95% CL	Upper 95% CL
Gross births (B_i^*)				
2006–2007	58.5	12.5	34.1	83.0
2007–2008	29.8	10.6	8.95	50.7
2008–Spring 2009	62.1	11.2	40.2	84.0
Net births (B_i)				
2006–2007	54.3	11.4	32.0	76.6
2007–2008	27.7	9.7	8.6	46.7
2008–Spring 2009	59.8	10.8	38.6	80.9
$B_i^* - B_i$				
2006–2007	4.3	1.1	2.1	6.4
2007–2008	2.1	0.9	0.4	4.0
2008–Spring 2009	2.3	0.4	1.6	3.1
Abundance (N_i)				
2006	91.6	12.0	68.0	115.2
2007	132.8	12.1	109.1	156.5
2008	141.6	11.8	118.5	164.7
Spring 2009	190.9	13.9	163.7	218.2
Gross population size (N^*)				
Total	242.1	9.8	222.8	261.3

TABLE 2. Estimates of real parameters from the best fit model [$\Phi(.)p(.)b(t)$]. Φ = probability of survival, p = capture probability, b_i = probability of entry, N = superpopulation size. Estimates for each parameter are presented with associated standard error (SE) and upper and lower 95% confidence limits (CL).

Parameter	Parameter estimate	SE	Lower 95% CL	Upper 95% CL
Φ	0.8578	0.0732	0.6504	0.9513
p	0.6436	0.0825	0.4715	0.7853
b_1	0.2327	0.0936	0.0978	0.4588
b_2	0.1185	0.0805	0.0288	0.3786
b_3	0.2562	0.0795	0.1320	0.4383
N	233.2914	18.0445	197.9241	268.6587

TABLE 4.   Corrected estimates of PIT tags deposited on Año Nuevo Island (ANI) by watershed of origin. Number of tags recovered on ANI from five central California watersheds between 2006 and Autumn 2010 are presented as: (1) total number and (2) percentage of total number of tags detected on ANI, (3) the number of tags deployed per watershed, and (4) the percentage of tags recovered on ANI relative to the number deployed in each watershed and all watersheds combined (deposition rate). NA = not applicable.

Watershed	Number of tags recovered on ANI	Percentage of total recovered on ANI (%)	Number of tags deployed	Deposition rate (%)
All combined	316		34,485	0.92
Waddell	63	19.9	1,576	4.00
Gazos	19	6.0	762	2.49
Scott	226	71.5	27,570	0.82
San Lorenzo	1	0.3	401	0.25
Soquel	3	0.9	4,176	0.07
Unidentified	4	1.3	NA	NA

DISCUSSION

We improved our minimum estimates of juvenile coho salmon and steelhead mortality from predation through a novel use of the POPAN formulation of the Jolly–Seber model (Jolly 1965; Seber 1965; Schwarz and Arnason 1996). During four complete scans of ANI conducted between autumn 2006 and spring 2009, use of the POPAN model to correct for tags deposited on the island but not detected during surveys resulted in an estimate of 242 tags deposited during the same period. This was an increase of 23% from the 196 tags that were physically detected on the island. By adding the number of tags detected during surveys conducted in autumn 2009 and 2010 and spring 2010 (120 tags), we obtained a new, minimum estimate of 362 PIT tags on ANI.

FIGURE 4.   Percentage (%) of total PIT tags originating in central California watersheds that were deposited on Año Nuevo Island (ANI). Data are derived from observed counts (filled circles) and model estimates (open circles). Watersheds of origin are plotted from left to right in increasing distance from ANI (Waddell Creek, 5.5 km; Gazos Creek, 6.6 km; Scott Creek, 12.0 km; San Lorenzo River, 33.0 km; Soquel Creek, 38.0 km).

This estimate of 362 tags still represents a minimum estimate of predation. For instance, the estimate does not account for a still unknown proportion of tags that were deposited away from ANI or that lost function during the process of ingestion and excretion (Collis et al. 2001; Ryan et al. 2001). Further, we were unable to use the POPAN method to calculate a corrected minimum estimate of predation when survey area was not consistent (autumn 2009 and 2010, spring 2009). Inclusion of these years would violate a key assumption of the model, resulting in an under- or overestimate of tag deposition (Arnason and Schwarz 2002). The estimate of 362 tags does not account for gross recruitment between sampling intervals after spring 2009. That is, we were unable to determine how many tags were deposited on ANI but were lost before sampling occurred during autumn 2009 or spring and autumn 2010 (Schwarz et al. 1993; Arnason and Schwarz 2002).

During years when effort and equipment performance was consistent, however, the mark–recapture approach we employed worked particularly well at ANI, where tags were not removed because of the clay-like substrate and risk of disturbance to seabirds and marine mammals. This method can be applied to future scans of ANI provided that effort and equipment performance are consistent among surveys. Although the corrected minimum estimates of predation we generated are applicable only to the system studied, the method we employed could be used in similar systems where PIT tags (or other individually unique tags that persist through digestion and excretion by predators) (1) are not removed from an area used frequently by predators, (2) are readily resighted, and (3) effort is consistent among surveys. Use of the POPAN model to generate a corrected minimum estimate of tag deposition and abundance on the island allowed us to account for tags that lost function after deposition on the island and tags that were not detected (due to tag breakage, signal interference, or burial out of the range of detection equipment), which have been cited as some of the common problems with using PIT tag recoveries to quantify predation on salmonids (Collis et al. 2001; Ryan et al. 2001).
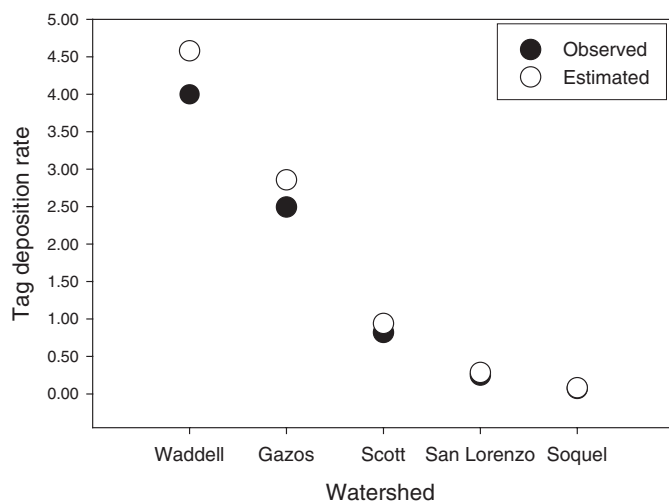
Salmonid migration and predator species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Juvenile steelhead out-migration												
Juvenile coho salmon out-migration												
Adult salmon return migration												
Western gulls												
Brandt's cormorants												
Brown pelicans							X					
California sea lions					X		X	X	X	X	X	

FIGURE 5. Out-migration periods of coho salmon and steelhead and return migration of adult coho salmon and steelhead (dark gray) with presence of piscivorous predators on Año Nuevo Island by breeding (black) and nonbreeding (light gray) seasons. Months (January [J] to December [D]) having the greatest abundance of California sea lions and month of mean peak count of brown pelicans are denoted with an "X."

The area of ANI where tags were most concentrated was within areas of the island heavily used by western gulls for breeding (Figure 1). Sea lions also use these areas; however, numbers vary greatly, and greatest abundance generally does not overlap in time with salmonid availability (Figure 5). Although some tags were located in areas used by Brandt's cormorants, these areas also were used by western gulls and California sea lions (P. Morris, personal communication; Figure 1). Brown pelicans roosted on the south terrace and central island in low numbers; the greatest numbers of brown pelicans roosted on the north terrace (P. Morris, personal communication), which is where the fewest tags were found (Figure 1).

Presence of tags from adult steelhead (mean FL, >400 mm) implies at least some deposition of tags by California sea lions. Western gulls, Brandt's cormorants, and brown pelicans eat small schooling fish (Pierotti and Annett 1995; Wallace and Wallace 1998; Shields 2002). Fish eaten by Brandt's cormorants breeding on southeast Farallon Island ranged from 4 to 200 mm total length (TL) (Boekelheide et al. 1990); brown pelicans in California and Mexico took similarly sized prey (range, 85–172 mm TL; Shields 2002). Sea lions were the only predator that used elevated portions of ANI where tags were found and were large enough to eat adult-sized salmonids. Steller sea lions were present on ANI; however, numbers were extremely low compared with numbers of California sea lions, so the probability of a Steller sea lion depositing a PIT tag on the island was believed to be extremely low (P. Morris, personal communication). Alternatively, gulls could have ingested PIT tags while scavenging a dead, PIT-tagged adult salmonid, but the probability of this occurring was extremely low because very few dead adult salmonids occurred in areas where they could be scavenged by gulls, and the occurrence of PIT tagged adults in these areas was even lower.

Several predators may be depositing PIT tags on ANI; however, we believe western gulls are responsible for the majority of tag deposition. The area of ANI where the most PIT tags were found was used by western gulls and California sea lions. Although recovery of some PIT tags deployed in adult steelhead indicates predation by sea lions, PIT tags have not been identified during diet analysis of California sea lions on ANI. Beginning in 2001, fecal samples (scats) collected from ANI were used to determine prey eaten by California sea lions. No PIT tags were found in fecal samples from California sea lions despite a large number of samples processed (100–150 per year between 2001–2007 and 371 between 2008 and 2011; M. Weise, Marine Mammals and Biological Oceanography Program, Office of Naval Research, personnel communication). If sea lions accounted for appreciable deposition of tags on ANI, we would expect that PIT tags would have been identified in at least some scat samples. Therefore it is unlikely that sea lions were responsible for deposition of the majority of tags in areas of ANI where western gulls and sea lions overlap. Of the predators that use areas of ANI where tags were located, western gulls were the only species visually observed eating juvenile salmonids during 198 h of observations conducted at the mouths of Scott and Waddell creeks as part of an associated study (Frechette 2010). Observed predation on juvenile salmonids by gulls occurred in freshwater before ocean entry (Frechette 2010). Recovery of archival temperature loggers deployed on juvenile salmonids also indicated predation occurred in freshwater (Hayes et al. 2012). The only predators that used ANI and were observed on the beach or in the estuary at Scott or Waddell creeks were western gulls and brown pelicans. Neither western gulls nor pelicans were observed upstream of bridges that cross Scott and Waddell creeks, approximately 100–200 m from where these creeks enter the ocean (D. Frechette, unpublished data). Therefore predation most probably occurred in the most downstream portion of the estuary or immediately after salmonids entered the ocean. Because the estuary is too shallow to support the plunge-diving foraging methods employed by brown pelicans, any predation by pelicans would have occurred after fish had entered the ocean. As discussed previously, few tags have been detected in the area of the island most heavily used by roosting brown pelicans (the north terrace), so it is still unlikely that PIT tags were deposited on ANI by pelicans. Unlike gulls and cormorants, however, brown pelicans do not cast

pellets (Shields 2002), so predation on juvenile salmonids could go unnoticed if tags were destroyed in the process of digestion.

Western gulls have been observed bathing, loafing, and drinking water at all six watersheds where PIT tags were deployed in coho salmon and steelhead (Table A.1.1); however, the majority of PIT tags on ANI were from fish tagged in the three watersheds in closest proximity to the island (Waddell, Gazos, and Scott creeks). Recoveries of PIT tags on ANI only are indicative of predation by the population of western gulls using ANI as a roosting and breeding site. Gulls eating salmonids at watersheds at greater distances from ANI (e.g., San Lorenzo, Soquel, and Aptos) may not use ANI for breeding and roosting and probably deposit tags elsewhere, resulting in an underestimation of total predation on central California salmonids. Although no PIT tags were deployed in Gazos and Aptos creeks or the San Lorenzo River during the years when sampling was conducted on ANI, we still feel it was appropriate to apply the correction factor to these watersheds to improve minimum estimates of predation because tags from all watersheds, regardless of year of deployment, were incorporated in the model.

The majority of PIT tags on ANI originated in steelhead (89%). In the Columbia River basin, consumption of steelhead by Caspian terns was greater than expected based on their availability relative to other salmonids, which may represent selectivity by terns for the larger, more energy-dense steelhead compared with other salmonids (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005). In central California, however, tagging efforts have focused on the more abundant steelhead, so interpretation of the relative susceptibility of coho salmon and steelhead must be approached with caution. Work is ongoing to further examine relative susceptibility of juvenile salmonids to predation (A.-M. K. Osterback, unpublished data). It was possible, however, to draw some conclusions of relative susceptibility of juvenile steelhead to predation from Scott Creek, where the greatest tagging effort has occurred. Steelhead tagged in the Scott Creek estuary represented a greater proportion of wild-reared steelhead on ANI than fish tagged upstream of estuary influence (Figure 3). These estuary-reared steelhead have the life history strategy with greatest effects on population persistence in coastal watersheds in central California (Bond et al. 2008; Hayes et al. 2011).

Watersheds in the central California study area experience a unique hydrodynamic regime. Rainfall occurs predominantly during winter. During dry summers, deposition of beach sand creates a sandbar across creek mouths, blocking the estuaries from the ocean and causing formation of freshwater lagoons, typically during summer and autumn (Shapovalov and Taft 1954). Whereas coho salmon generally migrate directly to sea each spring as smolts, steelhead in some central California watersheds have alternative life history strategies that take advantage of seasonally forming freshwater lagoons. While some steelhead smolts complete their spring migration to the ocean, many pause in the lagoon where they spend several months during the summer (Bond et al. 2008) before migrating back

upstream for the winter and performing a second downstream migration the following spring, ultimately entering the ocean a year later (Hayes et al. 2011). Lagoon-reared steelhead undergoing the second migration are greater in size (FL > 150 mm) than steelhead completing a first downstream migration (FL < 150 mm) (Bond et al. 2008; Hayes et al. 2011). Bond al. (2008) documented increased smolt-to-adult survival for juvenile steelhead that reared in the Scott Creek lagoon. Although larger lagoon-reared fish comprised approximately 95.5% of returning adults, they only were 8–48% of the estimated number of spring out-migrants (Bond et al. 2008). Conversely, smaller juvenile steelhead that migrated directly to sea comprised only 4.5% of the returning adult steelhead population but were the majority of spring out-migrants (Bond et al. 2008; Hayes et al. 2011). Because all PIT-tagging in the Scott Creek estuary occurred during the lagoon period, tags on ANI from estuary-reared steelhead represent fish that reared in the lagoon (S. A. Hayes and D. Frechette, unpublished data). Tags from lagoon-reared steelhead comprised 70% (93 of 133) of tags from wild-origin steelhead that originated in Scott Creek and were detected on ANI during our study period. Our results indicated, therefore, that western gulls breeding on ANI predominantly ate lagoon-reared steelhead, which contribute disproportionately to the returning adult population thereby exacerbating population declines for this ESA-listed species.

Considerable effort has been expended to estimate avian predation on salmonid smolts migrating out of the Columbia River system, with particular emphasis placed on breeding colonies of Caspian terns. Predation rates on juvenile salmonids by Caspian terns have been estimated for tern colonies throughout the Columbia River basin using recovery of PIT tags (Roby et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Not surprisingly, our corrected estimate of predation by western gulls breeding on ANI (0.92% of tagged salmonids) was less than the estimate of predation reported for a substantially larger Caspian tern colony on Rice Island in the Columbia River estuary. Based on recovery of PIT tags on Rice Island, Caspian terns ate 4.4% (95% CI, 4.2–4.6%) of salmonids that entered the Columbia River estuary during 1998. Caspian terns on Rice Island, however, were more numerous (8,766 breeding pairs) than were western gulls on ANI (mean = 1,019 breeding pairs between 1998 and 2007; PRBO, unpublished data). Our estimate was more comparable with the estimated percentage of salmonids eaten by terns nesting in two smaller colonies upstream of the Columbia River estuary. During 2001, Crescent Island (located in the mid-Columbia River basin approximately 510 km upstream from the river mouth) supported 664 pairs of Caspian terns, which ate 1.4% of the salmonids originating in the upper Columbia River (Antolos et al. 2005). In the upper Columbia River basin, 202–323 pairs of Caspian terns nesting at Potholes Reservoir ate between 0.03% and 0.38% of PIT-tagged salmonids (coho salmon, Chinook salmon *O. tshawytscha*, and steelhead combined) during the years 2003, 2005, and 2006 (Maranto et al. 2010).

In addition to colony size, avian foraging strategy may also explain differences in predation rates observed between Caspian tern colonies on the Columbia River and the western gull colony on ANI. Caspian terns and glaucous-winged gull *L. glaucescens* × western gull hybrids breeding on Rice Island had very different diets, despite breeding in the same location. On Rice Island, the diet of Caspian terns consisted of 74% salmonids (by mass). Glaucous-winged × western gull hybrids had a more diverse diet composed of only 11% salmonids (Collis et al. 2002). Juvenile salmonids migrating out of central California watersheds were probably buffered from predation by the generalist diet of western gulls, contributing to the lower predation rate observed for ANI (0.92%) compared with that observed for the Caspian tern colony at Crescent Island (1.4%, Antolos et al. 2005). Additionally, the Columbia River system is orders of magnitude larger than watersheds in central California; thus, species diversity and abundance of salmonids in the Columbia River basin is far greater than in small central California watersheds, and salmonids occur in the Columbia River basin year-round. In central California coastal streams, coho salmon and steelhead are only available to avian predators during part of the year (Figure 5). Increased abundance, species diversity, and overlap between avian predators and salmonid prey may allow Caspian terns and other avian predators in the Columbia River basin to specialize on salmonids in ways that are not possible in small coastal watersheds in central California, resulting in greater levels of predation observed in the substantially larger Columbia River basin.

Further, predation rates at Rice Island reported by Roby et al. (2003) were based on the estimated number of salmonids that entered the Columbia River estuary and were available to Caspian terns nesting on the island. Fish that did not survive in-river migration to the estuary were not included in calculation of predation rates (Roby et al. 2003). We were not able to separate mortality of juvenile salmonids occurring upstream from the estuary from predation occurring immediately before or after ocean entry. Our predation estimate was based simply on the proportion of tags detected on ANI relative to total tags deployed. We expect that our estimate of tag deposition would increase if we could account for this as-yet undocumented in-river mortality. Such in-river mortality may result from density-dependent effects or predation by species of birds that occur in the upper watershed (for example, common mergansers *Mergus merganser* or belted kingfishers *Ceryle alcyon*). Roby et al. (2003) demonstrated that use of a bioenergetics modeling approach to estimate predation rates produced greater estimates than use of PIT tag recoveries (Roby et al. 2003). Bioenergetics models generate estimates of total consumption of salmonids by a breeding colony of birds, whereas PIT tag recoveries represent minimum estimates of predation, as described previously (Collis et al. 2001; Ryan et al. 2001; Roby et al. 2003). Using a bioenergetics approach, Roby et al. (2003) estimated that 13% (95% CI, 9.31–16.9%) of salmonids that entered the Columbia River estuary were eaten by Caspian terns breeding on Rice Island during 1998, which was greater than double the percentage estimated using PIT tag recoveries. Application of a comparable bioenergetics technique may further improve our estimate of the impacts on central California salmonids by western gulls breeding on ANI.

Although our novel use of a mark–recapture model allowed us to create a corrected estimate of predation for threatened and endangered coho salmon and steelhead along the central California coast, it remains a minimum estimate. However, based on application of this correction factor, we estimated that minimum predation on salmonids by western gulls breeding on ANI was between 1% (Scott Creek) and 4.6% (Waddell Creek) of juveniles. This previously undocumented degree of predation on juvenile salmonids in central California was greater than expected, especially considering that recoveries of intact PIT tags from ANI were indicative of predation predominantly by one age-class (adults) of one species (western gulls) at one breeding site (ANI). Further, the majority of PIT tags that originated from Scott Creek and were detected on ANI were from estuary-reared steelhead, which comprise the majority of returning adults (Bond et al. 2008). Predation on juvenile steelhead by western gulls, therefore, may be particularly detrimental to Central Coast steelhead. The levels of predation presented in this paper indicate that predation may be one factor limiting recovery of these species in central California and warrants further attention as populations of salmonids continue to decrease.

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APPENDIX 1: SUPPLEMENTAL SAMPLING INFORMATION

TABLE A.1.1. Number of coho salmon and steelhead smolt PIT tags deployed in each watershed during each year and distance from Año Nuevo Island (ANI). County is given in parentheses; SCC = Santa Cruz County, SMC = San Mateo County.

Watershed	Distance from ANI (km)	Year	Number of tags deployed
Gazos (SMC)	6.6	2003	150
		2004	289
		2005	323
		Total	**762**
Waddell (SCC)	5.5	2006	159
		2008	720
		2009	697
		Total	**1,576**
Scott (SCC)	12.0	2003	2263
		2004	2359
		2005	1512
		2006	3585
		2007	2807
		2008	3877
		2009	7173
		2010	3907
		2011	87
		Total	**27,570**
San Lorenzo (SCC)	33.0	2004	140
		2005	261
		Total	**401**

TABLE A.1.1. Continued.

Watershed	Distance from ANI (km)	Year	Number of tags deployed
Soquel (SCC)	38.0	2003	228
		2004	438
		2005	963
		2006	871
		2007	617
		2008	227
		2009	311
		2010	521
		Total	**4,176**
Aptos (SCC)	41.0	2004	342
		2005	171
		Total	**513**
Total number of tags deployed			**34,485**

TABLE A.1.2. Date of trips (month/day/year) made to Año Nuevo Island to scan for coho salmon and steelhead smolt PIT tags (2006–2010). Surveys included in the POPAN model are in bold text.

Season scan completed	Date of trips
Autumn 2006	**11/16/2006**
	1/24/2007
Autumn 2007	**9/24/2007**
Autumn 2008	**9/10/2008**
	10/7/2008
	10/27/2008
	11/17/2008
	12/29/2008
Spring 2009	**4/21/2009**
	5/1/2009
Autumn 2009	11/23/2009
	12/29/2009
Spring 2010	3/22/2010
	4/14/2010
	4/28/2010
Autumn 2010	9/7/2011
	11/30/2011
	12/31/2011
	1/27/2011

TABLE A.2.1. Goodness-of-fit test statistics (Burnham et al. 1987) for the fully time-dependent POPAN model $[\Phi(t)p(t)b(t)]$. Test 3 relates to the assumption of homogeneous survival; Test 2 relates to the assumption of homogeneous capture.

Test	Component	χ^2	df	P
3	3.SR2	2.17	1	0.14
	3.SR3	1.91	1	0.16
	3.Sm2	10.04	1	0.001
2	2.c2	0.39	1	0.53

APPENDIX 2: SUPPLEMENTAL STATISTICAL AND MODELING INFORMATION

Unlike animals, PIT tags have the ability to last indefinitely. It was suspected that failure to meet component (2) (see text) of the assumption of homogeneous survival resulted from the great number of individuals that were detected on all sampling occasions ($n = 18$). To test whether lack of model fit stemmed from having a high number of individuals detected during all surveys, we decreased the number of individuals detected during all sampling occasions in steps of two individuals, then reran the POPAN model and tested for goodness of fit using Program RELEASE (Burnham et al. 1987) within the Program MARK framework (White and Burnham 1999). When the number of individuals detected during all four surveys was set at 10, the assumption of homogeneous survival was met (Test 3.Sm2, Table A.2.2) and the χ^2 goodness-of-fit test indicated that the model fit the data ($\chi^2 = 7.15$, $P = 0.1281$). Estimates of parameters (Φ_i, p_i, and N) from model sets based on the original data set and the data set with the reduced number of individuals were similar so we used the model set derived from the original data to estimate the parameters of interest (Φ_i, p_i, N, B_i^*, B_i, N_i, and N^*).

TABLE A.2.2. Goodness-of-fit test statistics (Burnham et al. 1987) for the fully time-dependent POPAN model $[\Phi(t)p(t)b(t)]$ for the case in which the number of tags detected during all four surveys was set at 10 individuals. Test 3 relates to the assumption of homogeneous survival; Test 2 relates to the assumption of homogeneous capture.

Test	Test component	χ^2	df	P
3	3.SR2	0.95	1	0.44
	3.SR3	0.85	1	0.35
	3.Sm2	4.85	1	0.03
2	2.c2	0.86	1	0.35